INFRAPOPULATION DYNAMICS OF PARELAPHOSTRONGYLUS TENUIS IN WHITE-TAILED DEER

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ABSTRACT

White-tailed deer (*Odocoileus virginianus*), of known age, collected in northeastern Minnesota (n=379) from November 1991 to May 1993 were examined for Parelaphostrongylus tenuis. Prevalence and intensity estimates were based on adult worms in the cranium and first-stage larvae in the feces of the same individuals. Prevalence of worms in the cranium was higher (82%) than prevalence of larvae in the feces (53%). The difference between these two measures was largely (78%) due to unisexual, occult infections. The spinal column does not seem to be an important site for adult P. tenuis since only one of 26 animals had a worm (immature) located there.

In fawns, the prevalence of larvae (35%) and adult worms (68%) was lower than in all older age classes (63%, 89%, respectively). The mean number of adult worms was lower in fawns (2.7) and yearlings (3.0) than in deer 7-15 yr (4.1). Conversely, the mean number of larvae in feces was higher in fawns (102 larvae/g) than in adults 2-6 (36 l/g) and 7-15 yr (36 l/g).

More larvae were passed in spring (mean of 77 l/g) than in fall (11 l/g) or winter (38 l/g). Mean fecundity was greater in fawns (52 larvae/g/female worm) than in adults 2-6 yr (15 l/g/f) and 7-15 yr (12 l/g/f). The sex ratio of worms did not change with increasing age of deer, nor did the ratio of worms in the sinuses to subdural space. The number of larvae in feces was not correlated with the number of female P. tenuis in the cranium, but was correlated with the ratio of

A smaller sample of white-tailed deer (n = 34) from an area where density reached 30 deer/km^2 was compared with animals from the study area where summer density was 3.7 deer/km^2. The mean number of adult worms in deer of all ages was similar in both areas (3.2 and 3.5, respectively), but animals in the high density area passed more larvae (94 and 57 l/g, respectively).

Results suggest that P. tenuis is long-lived and that deer infected in their first or second summer of life acquire few, if any, additional worms thereafter. A threshold number of adult worms in each deer limits infrapopulation larval production as deer density increases. Infrapopulation larval production, however, is highest in young animals and in the spring. Suprapopulation larval production will be affected by deer density, the proportion of young naive deer in a population and the ability of deer to produce an effective immune response to the parasite.

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TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

The meningeal worm, Parelaphostrongylus tenuis, is a common and widely distributed parasite of white-tailed deer (Odocoileus virginianus) in eastern North America (Anderson and Prestwood 1981, Comer et al. 1991, Anderson 1992). Infections in this normal definitive host are relatively benign but severe neurologic disorders and death can result in a variety of other ungulates (Anderson and Prestwood 1981). In areas where white-tailed deer are sympatric with moose and other susceptible ungulates, P. tenuis is an important management consideration. However, much remains to be learned about its biology and transmission within white-tailed deer populations before its importance as a pathogen to other species can be completely assessed.

The adult nematodes, living in the cranial venous blood sinuses and subdural space of deer, produce eggs that develop into first-stage larvae within the lungs of the definitive host, and are subsequently shed in the feces (Anderson 1963 and 1965). Larvae are found only in the mucus covering the outside of the fecal pellet (Lankester and Anderson 1968). Terrestrial snails and slugs are required intermediate hosts in which larvae from feces and soil develop to the infective stage. Infection of ruminants results from accidental ingestion of gastropods while eating vegetation.

The proportion of a deer herd infected (prevalence) and the mean number of parasites per infected deer (mean intensity) are likely important variables in

determining the rate of transmission of this parasite (Lankester 1987, Peterson and Lankester 1991). Which of these two variables best reflects the risk of infection to cervids is presently unclear. Saunders (1973) reported that where the prevalence of P. tenuis was high in white-tailed deer, moose densities were low. On the other hand, Whitlaw and Lankester (1994), in a wider study of co-habiting deer and moose in Ontario, found moose density to be independent of the prevalence of the parasite in deer but inversely related to the intensity of larvae in deer feces. Other authors have failed to find any consistent relationship between the prevalence of P. tenuis and the density of white-tailed deer (see Peterson and Lankester 1991).

Reported estimates of the prevalence of P. tenuis in deer vary considerably (Anderson and Prestwood 1981). Much of the apparent variation may be due, however, to differences in the two methods used to detect P. tenuis. Commonly, prevalence, as well as intensity, are determined by examining deer heads for adult worms. Heads have the added advantage of revealing the age of the host, but the procedure is laborious and recovering all of the worms present requires considerable skill and experience. Samples commonly are available only during the fall hunting season, and the age and sex of animals examined are usually dictated by game regulations. Alternatively, prevalence and intensity of P. tenuis are measured by examining feces for dorsal-spined larvae using the Baermann technique. Large samples can be examined with relative ease but the age of the deer, the number of different animals represented, and the identity of dorsal-

spined larvae recovered are often unknown.

Although one or the other of the two methods is usually used exclusively, a few authors have used both on the same animals. Anderson (1963), and Garner and Porter (1991) found that examination of feces detected more infections than examination of heads, while Bogaczyk et al. (1993) found the reverse. Larger sample sizes are probably needed to resolve these conflicting results and to allow a better understanding of the relationship between the number of adult worms present and the number of larvae released by infected deer.

Fundamental in understanding the dynamics of host-parasite systems is the rate of transmission of the parasite from one host to another (Anderson and May 1982). Initially, transmission rates are affected largely by the production of larvae by the definitive host, although climatic factors influencing larval survival and availability of intermediate hosts are undoubtedly important as well. Rezac et al. (1993), in modelling the infection of gastropods by first-stage protostrongylid larvae from sheep, concluded that the net rate of transmission from sheep to gastropods was directly proportional to the density of larvae times the density of gastropods. Schmitz and Nudds (1994) in constructing a theoretical model, also identified larval density as an important determinant, in understanding the transmission of P. tenuis. Larval density is a product of the number of animals releasing larvae and the number of larvae released per definitive host. In order to test hypothetical models of P. tenuis transmission, better empirical data on larval production and factors that affect it, are needed.

In the present study, a relatively large number of vehicle-killed deer of known age were available through much of the year from a population of known density. Numbers of adult P. tenuis in the head, and larvae in feces of the same animal, were counted. The purpose was to determine the relationships of deer age class, sex, density and season of the year to prevalence and intensity of P. tenuis. The relationships of number and location of female worms in the cranium to intensity of larvae in the feces were also examined. This enabled identification of factors, acting within individual deer, at the parasite infrapopulation level, that affect shedding of first-stage larvae by a white-tailed deer population, and thereby, rates of transmission in nature.

MATERIALS AND METHODS

Prevalence and intensity of P. tenuis in white-tailed deer were determined by examining the head (for adult worms) and feces (for larvae) from the same animal. Specimens were collected by Mr. Bill Peterson, Minnesota Department of Natural Resources, from Nov. 10, 1991 to May 31, 1993 in a traditional deer wintering area along the northwestern shore of Lake Superior, in the vicinity of Grand Marais, Minnesota. In summer, these deer range up to 20 or more kilometres inland and their density at this time of the year is estimated to be 3.7 deer/km^2 (Lenarz 1991, and 1993 unpubl. DNR report, Grand Rapids, MN). Most of the specimens were killed by vehicles between October and April (370); a few predator (3), hunter (2), and miscellaneous (4) kills were also included.

Heads, along with a fecal sample (approx. 20 grams) from the same animal, were stored frozen until examination. Sex and date of death were recorded for each individual. Age was determined by tooth eruption (fawns and yearlings) and cementum ring counts (adults) (Severinghaus 1949).

To determine if deer killed by vehicles and those in the rest of the population were similarly infected, the prevalence of larvae in fecal samples collected off snow, in March 1993 (n = 100) was compared to that from the road-killed sample collected in March 1993 (n = 50).

To investigate any effects of deer density on prevalence and intensity of infection, a sample of heads and feces from a high density deer area near

Minneapolis, MN was also examined. Thirty-four animals were shot in March 1993, in The Twin Cities Army Ammunition Plant (TCAAP), a fenced enclosure located approximately 10 km north of St. Paul. The year-round density of animals in this area was estimated to be 30 deer/km^2 (Jordan, pers. comm., University of Minnesota, Minneapolis, MN).

At necropsy, heads were cut sagitally, while still frozen, using a butcher's bandsaw and allowed to thaw for at least 24 hours. Shearing the hair on the dorsal surface of the head using animal clippers prevented the saw blade from jamming. Only heads free from gunshot wounds, or skull fractures due to vehicle collision, were examined for adult P. tenuis. After thawing, the two halves of the brain were removed from the cranium and the surface and sulci were examined. Removal of the brain allowed examination of the exposed inner surface of the dura. All tissues and surfaces were examined for worms at 1.5-12.5X. Subsequently, the dura was stripped from the brain case and all venous blood sinuses, including the cavernous, intercavernous, transverse and sagittal sinuses were cut open in saline and examined at 6.4 to 40X. Toothed forceps inserted into foramena along cranial nerves, were gently extracted to remove any worms that might be present.

The oral cavity and pharynx of some heads were examined for larvae using a modification of the Baermann procedure in order to determine if detection of larvae here correlated with what was found in the feces of the same animal. The back of the oral cavity in the vicinity of the epiglottis (throat), in each half of the

cut head, was doused with water. Rinsings were drained into a glass funnel. The funnel, with a short length of neoprene hose and clamp at the bottom, was covered with 2 mm mesh screening to catch any hair and undigested food particles. After settling for at least one hour, the sediment was drained from the funnel into a Syracuse watch glass (54 mm diam.) with a grid etched on the bottom and examined for larvae.

Data recorded for each head included number and sex of nematodes (estimated from the number of intact worms plus the number of additional matched anterior and posterior ends of broken worms), presence of grossly visible lesions, and location of worms. Sex of broken worms was determined by presence of eggs or sperm (100X). A sample of intact worms was measured with the aid of a drawing tube at 100X magnification and preserved in 10% glycerine in 70% ethanol.

The location of adult worms, whether in the cranial subdural space, any of three venous blood sinuses, or in the epidural space, was recorded. Individually the locations were: 1) subdural space over and around the cerebral hemispheres (including the surface of the cerebrum, the dural surfaces in that area and along cranial nerves), 2) subdural space over and around the cerebellum (including the surface of the cerebellum, the dural surfaces in that area and along cranial nerves), 3) on the tentorium cerebelli (the dura forming the septum between the cerebrum and cerebellum), 4) on the falx cerebri (the dura lying in the longitudinal fissure between the two cerebral hemispheres), 5) on the diaphragm

sellae (the dura over the cavernous sinuses), 6) in the cavernous and intercavernous sinuses, 7) in transverse sinuses, 8) in the sagittal sinus, and 9) the epidural space.

To determine if any adult P. tenuis reside in the spinal canal, the head and entire spinal column of 26 deer were examined. The frozen column was initially cut into 4 equal segments, each of which was cut sagitally with a bandsaw and allowed to thaw for 24 hours. The cord was removed by severing the spinal nerves; the leptomeningeal surfaces and the spinal dura mater were examined using a stereoscope at 1.5-12.5X. Following visual examination, all tissues were agitated vigorously in water in a settling flask. Flasks were later decanted and the sediment examined for worms. The epidural space was examined by scraping away fat deposits with forceps. Toothed forceps were inserted into foramena and gently pulled out along spinal nerves to extract any hidden worms.

Weighed samples of feces from each deer were examined for dorsal-spined, first-stage larvae using the Baermann technique as described by Peterson and Lankester (1991). Larvae were counted and expressed as numbers of larvae per gram of fresh feces.

Deer are assumed to have been born June 1. Data were analyzed using four grouped age classes: fawns (<1 yr, collected June 1 through to May 31); yearlings (1 yr, in their 2nd year of life); and 2 adult age classes (2-6 years and 7-15 years). Analyses of seasonal differences were done by pooling data according to summer (June-Aug.), fall (Sept.-Nov.), winter (Dec.-Feb.), and spring (Mar.-

May). However, since sample sizes during the summer (n = 4) were low, deer collected in this period were omitted from seasonal analyses.

Data were analyzed using the Statistical Package for the Social Sciences (SPSS) and SAS. Significance for all analyses was determined at $p < 0.05$. Statistical analyses included heterogeneity Chi-square tests to detect differences in prevalence of P. tenuis by age class and sex of deer and year of sampling. Standard univariate Chi-square tests were used to detect differences in prevalence by age class and season of sampling, and to detect any differences in the number of worms in the sinuses to those in the subdural space, in the proportion of unisexual infections and, in the number of female to male worms by age class. An attempt was made to normalize the data set for number of worms (total and female) in the cranium and number of larvae per gram of feces by using log, ln, square root, arcsine, arctan and inverse hyperbolic sine transformations. None normalized the data. As a result, the Mann-Whitney U-test was used to detect any differences in intensity of infection by sex of deer and year of collection. Kruskal-Wallis (H-statistic) and multiple comparisons (Zar 1984) were used to detect differences in mean intensity of infection and mean fecundity between age classes of deer and season of the year. Spearman's rank correlation coefficients (r_s) were calculated for relationships between mean intensity of infection (based on adults and larvae) and age of deer, and between the mean number of larvae per gram of feces, number of female worms in the cranium, and location of female worms (sinus or subdural space) and between age of deer and mean fecundity.

RESULTS

The heads and feces from 379 deer were examined for evidence of P. tenuis infection. Adult P. tenuis were present in the cranium of 82% while only 53% had dorsal-spined larvae in their feces. Overall, 84% had either worms in the cranium and/or larvae in their feces. All but two of 45 deer older than six years had worms in the cranium (Table 1).

Infections with P. tenuis were manifested in different ways (Table 2). Of deer passing larvae, most (150) had both sexes of worm present, but in 43 (29 with only females, 14 only males) only one sex was found, and no worms were detected in nine. One hundred and eighteen deer had occult infections, in which adult worms [either only one sex (92) or both sexes (26)] were found in the cranium but no larvae were present in the feces. Of the 26 with both sexes present, 18 (69%) were younger than two years, and, therefore, may not have been infected long enough for worms to mate and for larvae to appear in the feces. Seven of the 26 animals, ranging in age from one to six yrs, were killed in March and early April, and would have acquired their infection at least four to five months earlier.

Prevalence of adult worms in the cranium was affected by age of deer regardless of sex or year of collection. The heterogeneity chi-square test indicated no differences in prevalence between collection years (X^2 = 1.1, df = 3, P > .05), or between sexes (X^2 = -4.07, df = 1, P > .05). Therefore, year and sex data were pooled for further analyses. Prevalence of adult worms in the

Table 1. Prevalence (%) of Parelaphostrongylus tenuis by age of white-tailed deer collected in northeastern Minnesota, Nov. 1991 - May 1993.

Age	Number of deer examined	Prevalence (%)		Overall prevalence (n)[a]
		Adults in heads (n)	Larvae in feces (n)	
<1	132	68 (90)[b]	35 (46)	71 (93)
1	85	87 (74)	58 (49)	91 (77)
2-6	117	89 (104)	66 (77)	92 (107)
7-15	45	96 (43)	67 (30)	96 (43)
Total	379	82 (311)	53 (202)	84 (320)

[a] percent of deer infected with larvae in the feces and/or adult worms in the cranium

[b] (number of deer infected)

Table 2. Examination of white-tailed deer from northeastern Minnesota (Nov. 1991 - May 1993) for Parelaphostrongylus tenuis.

Deer with P. tenuis					No evidence of P. tenuis	Total
Adults in heads				No adults in heads		
Bisexual infection		Unisexual infection				
Passing larvae	Not passing larvae	Passing larvae	Not passing larvae	Passing larvae		
150	26	43	92	9	59	379

cranium was lower in fawns (68%) than in the three older age classes (89%, X^2 = 26.5, P < .001), which did not differ from each other (X^2 = 2.3, P = .31) (Table 1). Prevalence of worms varied with season in the fawn age class (X^2 =9.2, P < .009), but not in animals older than one year (X^2 = .68, P = .71). Within fawns, prevalence of worms was lower in fall (43%) than in winter (68%, X^2 = 3.84, P = .049) and in spring (79%, X^2 = 9.29, P = .002) (Table 3).

Similarly, prevalence of larvae in the feces was affected by age of deer regardless of sex or year of collection. The heterogeneity chi-square test indicated no difference in prevalence between collection years (X^2 = 0.2, df = 3, P > .05) or between sexes (X^2 = .18, df = 1, p > .05). Prevalence of larvae was lower in fawns (35%) than in the three older age classes (63%, X^2 = 27.7, P < .001), which did not differ from each other (X^2 = 1.7, P = .43) (Table 1). Prevalence of larvae in the feces varied with season in the fawn age class (X^2 = 21.48, P < .001), but not in animals older than one year (X^2 = 3.44, P = .17). Within fawns, prevalence of larvae was lower in fall (5%) than in winter (25%, X^2= 4.2, P = .03) and in spring (58%, X^2 = 16.6, P < .001) (Table 3).

The prevalence of larvae in the feces collected at random off snow in March (71%) (n=100) did not differ from the prevalence in feces of animals killed by vehicles (58%) (n=50) in that same month (X^2 = 2.54, p = .16).

Intensity of larvae in the feces and adult worms in the cranium of infected animals did not differ between years or sex of deer. Year had no effect on the mean number of worms in the cranium of infected deer (fawns, U = 830.5, P =

Table 3. Seasonal prevalence and mean intensity of Parelaphostrongylus tenuis in heads and feces of white-tailed deer collected in northeastern Minnesota, Nov. 1991 - May 1993.

Age	Season	Prevalence (%)				Intensity	
		Adults in heads		Larvae in feces		Adults in heads	Larvae in feces (/g)
		%	(n)[a]	%	(n)[a]	Mean ± SD	Mean ± SD
<1	Summer	N/A	(0/0)	N/A	(0/0)	N/A	N/A
	Fall	43	(9/21)	5	(1/21)	1.8 ± 0.9	0.2 ± N/A
	Winter	68	(40/59)	25	(15/59)	2.7 ± 2.0	52.3 ± 58.1
	Spring	79	(41/52)	58	(30/52)	2.8 ± 1.8	131.8 ± 133.3
	Total	68	(90/132)	35	(46/132)	2.7 ± 1.8	102.9 ± 118.9
>1	Summer	75	(3/4)	50	(2/4)	1.7 ± 0.6	39.8 ± 53.8
	Fall	93	(28/30)	56	(17/30)	3.5 ± 2.5	11.2 ± 13.2
	Winter	88	(77/88)	60	(53/88)	3.8 ± 2.5	33.1 ± 41.2
	Spring	90	(113/125)	67	(84/125)	3.2 ± 2.2	57.0 ± 64.4
	Total	89	(221/247)	63	(156/247)	3.4 ± 2.4	43.5 ± 55.3
Overall	Summer	75	(3/4)	50	(2/4)	1.6 ± 0.6	39.8 ± 53.8
	Fall	73	(37/51)	35	(18/51)	3.1 ± 2.3	10.6 ± 13.0
	Winter	80	(117/147)	46	(68/147)	3.4 ± 2.4	37.5 ± 45.7
	Spring	87	(154/177)	64	(114/177)	3.1 ± 2.1	76.8 ± 93.5
	Total	82	(311/379)	53	(202/379)	3.2 ± 2.2	57.1 ± 78.4

[a] (Number of animals infected/number of animals examined)

.23; >1 yr, U = 5201, P = .44) nor on the mean number of larvae per gram of feces (fawns, U = 205, P = .65; >1, U = 1166, P = .30). Sex of deer had no effect on the mean number of worms in the cranium (U = 7834, P = .10) nor on the mean number of larvae per gram of feces (U = 3425, P = .44). Therefore, year and sex data were pooled for further analyses.

Intensity of infection, as measured by the mean number of worms per infected deer, increased with the age of deer (r_s = 0.20, P < .001) (Table 4). The mean number of worms in the cranium was lower in fawns (2.7) and yearlings (3.0) than it was in adults 7-15 yr (4.1); but adults 2-6 yr (3.5) did not differ from other age classes (H = 14.6, P = .002). Conversely, intensity of infection as measured by the mean number of larvae per gram of feces (in only those deer that were passing larvae) decreased with the age of deer (r_s = -0.28, P < .001). The mean number of larvae per gram of feces was greater in fawns (102.9 l/g) than in adults 2-6 yr (36.2 l/g) and 7-15 (35.6 l/g); but yearlings (59.8 l/g) did not differ from the two adult age classes (H = 13.17, P = .004) (Table 4).

Animals passed more larvae in spring (mean 77 l/g) than in fall (11 l/g) and winter (38 l/g) (H = 17.6, P = .0002). On the other hand, the mean number of adult worms in heads did not vary with season (H = 3.2, P = .20) (Table 3).

The intensity of larvae in feces was not correlated with the number of adult female P. tenuis in the cranium (includes only those animals that were passing larvae and had female P. tenuis in their heads) (r_s = .11, P = .06). However, intensity of larvae in feces was correlated with location of female

Table 4. Mean intensity of adult Parelaphostrongylus tenuis and larvae/gram of feces in white-tailed deer collected in northeastern Minnesota, Nov. 1991 - May 1993.

Age	Adults in heads	Larvae in feces
	Mean ± SD	Mean ± SD
<1	2.7 ± 1.8	102.9 ± 118.9
1	3.0 ± 2.1	59.8 ± 64.7
2-6	3.5 ± 2.5	36.2 ± 45.9
7-15	4.1 ± 2.5	35.6 ± 60.0
Total	3.2 ± 2.2	57.1 ± 78.4

worms (r_s = .58, P < .001); as the ratio of female worms in the venous sinuses to subdural space increased, so did the number of larvae released in the feces.

Mean fecundity of female worms (mean number of larvae/gram of feces/female worm in only deer with both female P. tenuis in their heads and larvae in their feces) decreased with the age of deer (r_s = -.34, P < .001) (Table 5). Mean fecundity was greater in fawns (51.6 larvae/gram of feces/female worm) than in adults 2-6 yr (14.6 l/g/f) and 7-15 yr (11.6 l/g/f); but yearlings (28 l/g/f) did not differ from fawns or the two adult age classes (H = 19.13, P = .0003). Mean fecundity was greater in spring (44.1 l/g/f) than in fall (6.3 l/g/f) (H = 18.37, P = .0001).

Although the highest proportion of unisexual infections (40%) was found in the fawn age class, it did not change significantly with age of deer (yearlings = 28%; 2-6 yr = 24%; 7-15 yr = 23%; X^2 = 7.07, P > .05). Bisexual, occult infections were most frequent in fawns (12%) (Table 6).

The overall sex ratio of adult worms was 1.5 females:1 male. In all age classes of deer, female worms outnumbered males, but the sex ratio did not change with age of deer (r_s = 2.33, P > .05) (Table 7).

Of the nine regions searched in the cranium, most worms were found in the cavernous, venous blood sinuses (39%, n = 388); the dura over the cerebrum was the second most frequented site (24%, n = 239). The three venous blood sinuses, collectively, were occupied more frequently (58%, n = 578) than the subdural (40%, n = 403) or epidural space (1%, n = 10) (Table 8). The ratio of

Table 5. Fecundity of female Parelaphostrongylus tenuis by age of white-tailed deer collected in northeastern Minnesota, Nov. 1991 - May 1993.

Age of deer	Mean no. of female worms/deer ± SD	Mean no. of larvae/g ± SD	Mean fecundity[a] ± SD
<1	2.0 ± 1.2 (79/39)[b]	103.2 ± 105.2	51.6 ± 64.8
1	2.3 ± 1.4 (99/44)	64.4 ± 66.6	28.0 ± 30.7
2-6	2.5 ± 1.8 (171/69)	36.5 ± 46.3	14.6 ± 26.3
7-15	3.3 ± 2.0 (89/27)	38.3 ± 59.4	11.6 ± 27.9
Total	2.4 ± 1.7 (438/179)	58.1 ± 74.1	24.2 ± 40.8

[a] Mean number of larvae per gram of feces/female worm.

[b] Mean (total number of female worms/number of deer with female worms in their head and larvae in their feces).

Table 5. Fecundity of female Parelaphostrongylus tenuis by age of white-tailed deer collected in northeastern Minnesota, Nov. 1991 - May 1993.

Age of deer	Mean no. of female worms/deer ± SD	Mean no. of larvae/g ± SD	Mean fecundity[a] ± SD
<1	2.0 ± 1.2 (79/39)[b]	103.2 ± 105.2	51.6 ± 64.8
1	2.3 ± 1.4 (99/44)	64.4 ± 66.6	28.0 ± 30.7
2-6	2.5 ± 1.8 (171/69)	36.5 ± 46.3	14.6 ± 26.3
7-15	3.3 ± 2.0 (89/27)	38.3 ± 59.4	11.6 ± 27.9
Total	2.4 ± 1.7 (438/179)	58.1 ± 74.1	24.2 ± 40.8

[a] Mean number of larvae per gram of feces/female worm.

[b] Mean (total number of female worms/number of deer with female worms in their head and larvae in their feces).

Table 7. Sex ratio of Parelaphostrongylus tenuis by age class of white-tailed deer collected in northeastern Minnesota, Nov. 1991-May 1993.

Age	Total no. of female worms	Total no. of male worms	Ratio of f:m
<1	133	101	1.3:1
1	134	88	1.5:1
2-6	214	145	1.5:1
7-15	113	63	1.8:1
Total	594	397	1.5:1

Table 8. Location of female and male Parelaphostrongylus tenuis (n=991) in crania of white-tailed deer (n=379) collected in northeastern Minnesota, Nov. 1991-May 1993.

Location	Female	% of total females	Male	% of total males	Total
Subdural space					
Around cerebrum	140	23.5	99	24.9	239
Around cerebellum	16	2.7	18	4.5	34
Falx dura	10	1.6	3	0.7	13
Tentorial dura	42	7.0	27	6.7	69
Diaphragm sellae	35	5.9	13	3.2	48
Total	238	40.1	154	38.4	403
Venous sinuses					
Sagittal sinus	51	8.5	34	8.5	85
Transverse sinus	71	11.9	34	8.5	105
Cavernous sinuses	225	37.9	163	40.6	388
Total	347	58.4	231	57.6	578
Epidural space	4	0.7	6	1.5	10
Overall	594		397		991

worms in the sinus to subdural space did not change with age of deer (X^2 = 7.2, P > .05) (Table 9).

Both the heads and spinal canals of 26 animals older than one year were examined. Fifteen of these animals were passing larvae in their feces and 11 were not. Of the fifteen, 10 had bisexual infections in the cranium, three had unisexual infections and two had no worms in the cranium nor in the spinal canal. Only one female, subadult worm was found in the spinal canal of a three-year-old female that had larvae in the feces and worms in the cranium and was killed on Jan. 15, 1993. The worm was flushed from the canal and the precise location was not determined; it probably inhabited the spinal subdural space.

A total of 62 throat washes were performed. All of twenty-six animals with bisexual infections and larvae in the feces also had larvae in the oral cavity and throat. Ten animals with bisexual infections, but without larvae in the feces, also had no larvae in throat washes. Of 24 animals with unisexual infections, six had no larvae in the feces and negative throat washes, and 18 had larvae in both the feces and the throat wash. Two animals with no worms in the cranium had no larvae in the feces or in throat washes. In the absence of fecal samples, throat washes can be relied upon to detect animals passing larvae.

Most of the worms located on the dura were partially embedded under fibrinous strands associated with little, if any, inflammatory exudate. In 22 deer, the dura was thickened and covered by a yellowish-red exudate in the vicinity of the worms. All but five of these latter animals were older than two years. In 29

Table 9. Numbers of Parelaphostrongylus tenuis found in venous blood sinuses and the subdural space by age class of white-tailed deer collected in northeastern Minnesota, Nov. 1991 - May 1993.

Age	No. deer infected	Total worms	Number of worms in the subdural space	Number of worms in the sinuses	Ratio[a]
<1	90	234	108	125	1.2:1
1	74	221	80	138	1.7:1
2-6	104	359	136	220	1.6:1
7-15	43	177	79	95	1.2:1
Total	311	991	403	578	1.4:1

[a] Ratio of worms in sinuses to subdural space

deer, almost all of which were older than two years, the sagittal and transverse blood sinuses were occluded with masses of up to 10 worms. Thickening of the sinus walls and inflammatory exudate were invariably associated with such masses. When the exudate was pressed between glass plates and examined under the stereo-microscope (40 X), numerous eggs and active larvae were seen. Three adult deer had worms located under the pia-arachnoid with portions of the worms penetrating between sulci of the brain, but they did not appear to penetrate the neural tissue.

Thirty-four additional deer heads and feces were examined from a location where deer density was known to be unusually high (TCAAP). The prevalence of adult worms did not differ significantly between the TCAAP (94%) and Grand Marais animals (82%) (X^2 = 1.8 , P = .17). However, prevalence of larvae was higher in the TCAAP animals (77%) than in those from Grand Marais (53%) (X^2 = 6.7, P = .01) (Table 10).

The mean number of adult worms in the Grand Marais animals (3.2) was not different from the TCAAP animals (3.5) (U = 4023.5, P = .12), but TCAAP animals (93.8 l/g) passed a greater mean number of larvae than those from Grand Marais (57.1 l/g) (U = 1802.5, P = .01) (Table 6). Moreover, mean fecundity of female worms was higher in the TCAAP animals (42.6 l/g/f) than in those from Grand Marais (24.2 l/g/f, U = 2326.0, P = .002).

Table 10. Prevalence (%) and mean intensity of Parelaphostrongylus tenuis in heads and feces of white-tailed deer collected from two localities of differing deer densities: Grand Marais and TCAAP.

Location	Deer/km^2	Age	No. deer examined	Adults in heads		Larvae in feces		Overall prevalence[a]
				Prevalence (%)	Mean intensity ± SD	Prevalence (%)	Mean intensity ± SD (n)	
Grand Marais								
		<1	132	68	2.7 ± 1.8	35	102.9 ± 118.6 (46)	71
	3.7	>1	247	90	3.4 ± 2.4	63	43.5 ± 55.3 (156)	92
		Total	379	82	3.2 ± 2.2	53	57.1 ± 78.4 (202)	84
TCAAP								
		<1	8	88	3.7 ± 2.6	62	134.0 ± 73.5 (5)	88
	30	>1	26	96	3.5 ± 1.6	81	84.1 ± 83.0 (21)	96
		Total	34	94	3.5 ± 1.8	77	93.8 ± 82.3 (26)	94

[a] percent of deer infected with larvae in the feces and/or adult worms in the cranuim

DISCUSSION

Of the 379 white-tailed deer examined, 82% had adult P. tenuis in the cranium, but only 53% were passing larvae in their feces. Almost one-third of the infections in deer were occult since no larvae were present in feces. Some occult infections in fawns and yearlings, were probably pre-patent, but in older animals, most were sterile because parasites of only one sex were present.

Young deer were rapidly infected during their first two summers of life. Nearly 90% of yearlings had worms in the cranium. Other authors have reported similar rapid increases in prevalence of P. tenuis within the first few years of a deer's life (Anderson 1963, Behrend and Witter 1968, Behrend 1970, Beaudoin et al. 1970, Thurston and Strout 1978, Dew 1988, Garner and Porter 1991, Bogaczyk et al. 1993). Samuel et al. (1985), studied a closely related nematode, P. odocoilei, in mule deer (Odocoileus hemionus) and found that fawns first picked up infected gastropods in September, after arriving on their wintering grounds. By January, 100% of the fawns were passing larvae in their droppings.

Prevalence of infection did not differ significantly among older age classes of deer but eventually most animals became infected. All but 2 of 45 deer 7-15 years old had worms in the cranium. Karns (1967), was the first to suggest that almost all deer in an enzootic area probably become infected with P. tenuis. Although his sample size was limited and feces were not examined, adult P. tenuis occurred in the head of every one of 19 deer older than 4.5 years. Behrend and

Witter (1968) reported similar results. Other reports of many older deer being free of infection (Anderson 1963, Beaudoin et al. 1970) may be due to incomplete searches of the cranium for adult worms.

Peterson and Lankester (1991) studied the same Grand Marais deer population, but examined only feces. They found a similar pattern of infection. The prevalence of larvae peaked in yearlings at 57% but thereafter increased little in older animals. They found it difficult to explain why nearly half of the older animals appeared to be free of infection. My results demonstrate that most older animals are infected, but deer with unisexual infections fail to pass larvae.

Prevalence of P. tenuis is greater in spring than in the preceding fall or winter, only in fawns. Although worms appeared in the cranium of fawns as early as September, larvae did not appear in the feces of any fawns until mid-December, with the majority beginning to shed larvae in January. This is because it takes at least 50 days for worms to reach the cranium and at least 90 days for larvae to appear in the feces (Anderson 1963). Therefore, fawns, over their first year of life, will develop more patent infections as the year progresses. No change in prevalence with season is observed in older animals, because most are already infected. Similarly, Garner and Porter (1991) found no difference in the prevalence of worms in the cranium by season.

The pre-patent period for P. tenuis in naturally infected deer may occasionally be longer than the 80-91 days observed in experimental infections (Anderson 1963 and 1965). Of the 26 animals examined here with bisexual,

occult infections, seven were killed in early March to April. Assuming that the opportunity to pick up infected gastropods ceases after mid-November snow-falls, then these animals would have been infected for at least four to five months and yet were still not passing larvae. Samuel et al. (1992) observed pre-patent periods from 88-128 days, in experimental infections using low doses of infective P. tenuis larvae. Infection in nature probably involves small numbers of infective larvae, similarly increasing the period required for patency.

Neither the prevalence of adults in the cranium nor prevalence of larvae in the feces were correlated with the sex of deer. Garner and Porter (1991) also found no significant difference in prevalence between males and females, however others have reported that males tend to be infected more than females (Thurston and Strout 1978) or females more than males (Dudak et al. 1965). Gilbert (1973) suggested that sex-related behavioral differences in cover-type selection during fawn rearing may predispose adult females to greater contact with infected gastropods. Results reported here, however, show that most female deer become infected before they ever rear young. The lack of consistent results regarding infection rates by sex seems to suggest that both sexes generally are equally infected (Lankester 1987).

Comparisons of the prevalence of P. tenuis among deer populations should be made using similar data resulting from either examination of heads for adult worms or feces for larvae. Moreover, age composition of the deer herds being compared should also be similar. Samples of hunter-killed white-tailed deer

collected in fall, usually include a large number of fawns. Some animals in this age group will not yet have encountered the parasite while others will contain only migrating worms not yet visible in the cranium. Fawns killed in late winter or early spring will most accurately reveal the rate of parasite acquisition during the first summer on range.

The kind of information sought will dictate which data collection method should be utilized. Heads alone provide the most accurate measure of how many deer in a population are infected. The possibility that some adults reside in the spinal canal can be ignored. Only immature, presumably newly acquired, worms occurred in the canal and with very low frequency. Thurston and Strout (1978), similarly, found only 0.8% of deer with adult P. tenuis on the spinal dura mater. Examination of feces, on the other hand, provides a measure of the number of deer passing larvae and of mean larval intensity and, thereby, estimates of the total production of first-stage larvae by the parasite suprapopulation. A serious problem exists, however, in interpreting results of fecal analyses. Other species of metastrongyloids in white-tailed deer produce dorsal-spined larvae indistinguishable from those of P. tenuis (Pybus and Samuel 1981, Lankester and Hauta 1989). Their presence must be either excluded or accounted for.

Results presented here suggest that P. tenuis may live as long as their host. An immune response probably minimizes the acquisition of additional worms beyond those acquired in the animals' first two summers of life. Evidence for this is provided by the observations that the mean number of adult worms, their

sex ratio, and the proportion of unisexual infections, all remain unchanged in deer from 2-15 years old. Several other authors report that the mean intensity of P. tenuis is similar in deer older than one year (Behrend 1970, Gilbert 1973, Brown 1983, Bogaczyk et al. 1993, Jarvinen and Hedberg 1993). Also, worms in older deer are often found surrounded by exudate and adhering to the meninges, rather than being free on the surface, suggesting that they have been present for some time. Alternatively, P. tenuis may live only a few years, and balanced mortality and recruitment rates could establish a constant intensity of infection over time. However, studies on other species in the family Protostrongylidae strengthen the suggestion that P. tenuis lives for several years. Watson (1984) reported that Elaphostrongylus cervi lives for up to six years in red deer (Cervus elaphus elaphus) and Samuel (pers. comm.) had an experimentally infected mule deer passing larvae of P. odocoilei for 11 years.

If P. tenuis is equally long-lived, the first few infective larvae to be ingested by a deer must initiate a protective immunity against further infection, in which case, worms in older deer would themselves be older. Prestwood and Nettles (1977) demonstrated that white-tailed deer develop an immunity to P. andersoni and resist subsequent challenge infections. It is also known that deer produce a strong eosinophilic response upon infection with P. tenuis (Anderson and Strelive 1967).

Bull (1964) reported that the prevalence of Taenia pisiformis cysticerci in its rabbit intermediate host, Oryctolagus cuniculus, increased with increasing host

age, but mean intensity remained constant once a certain threshold number of cysticerci was reached in each rabbit. They concluded that the number of eggs initially consumed determined the long-term size of the infrapopulation since subsequent exposure did not increase the infrapopulation size.

The low number of adult worms present in deer may result from ingesting only a few infected gastropods over a relatively short period of time. Although the success rate of individual infective larvae reaching maturity in deer is unknown, few may have to be ingested to establish the relatively low number of persistent worms present. It is known that most naturally infected gastropods harbour fewer than three infective P. tenuis larvae each (Lankester and Anderson 1968). In the northern part of their range, white-tailed deer fawns have only four to five months to acquire infection before the snow comes. During winter, sufficient immune response may develop to prevent appreciable future infection. Most animals escaping infection in their first summer become infected in their second. Deer in southern areas have a slightly greater mean number of worms per animal than northern deer (Anderson and Prestwood 1981). Possibly, a transmission period extending through most of the year in southern regions allows them to acquire more infective larvae before immunity develops.

Occasionally heavily infected gastropods are found, as was the case of one Deroceras laeve from Navy Island containing 97 larvae (Lankester and Anderson 1968). The few massive infections of P. tenuis reported in deer (Prestwood and Smith 1969, Prestwood 1970), probably resulted from ingesting single heavily

infected gastropods, or several over a short interval, rather than accumulating worms over an extended period.

A number of animals (52) passed larvae in their feces but did not have a bisexual infection in their cranium. Although some worms may have been overlooked, other suggestions are possible. Since the spinal canal is not an important site for adult worms, possibly some are swept to other locations via the circulatory system. This probably happened to the type specimen of P. tenuis which was not found in the cranium but in the lungs (Dougherty 1945). This first specimen was a male. Since males are smaller than females (Carreno and Lankester 1993), and because the number of female worms outnumbered males in all age classes of deer, it is conceivable that males are more prone to being swept from the cranial venous blood sinuses to other locations in the body. The nine deer with no adults in the head but larvae in feces, could have been infected with P. andersoni. The adults of this species occur in muscles and the larvae are indistinguishable from those of P. tenuis. However, Peterson and Lankester (1991), after examining the longissimus dorsi muscles of 35 deer from Grand Marais, concluded that P. andersoni was absent or infrequent in this population.

The intensity of larvae in the feces is affected by a number of factors, one of which appears to be age of the host. The greatest numbers of larvae are released by young, recently infected deer and in older deer, larval production declines. Anderson (1963) suggested that the higher larval output in fawns was due to recent infection of naive animals. Declining larval production by older

deer could result from decreased egg output by older female worms and/or increased host immune response to eggs and larvae developing in the lungs. Individual effects of these two components could not be separated in my measurement of female fecundity. Fecundity was calculated here by apportioning larvae counted in feces with the number of female worms in the head. Nonetheless, despite having fewer adult worms, young deer produced the greatest number of first-stage larvae per female worm. In older deer the number of larvae passed per female worm was lower.

Larval output is also affected by season, increasing during spring. This could be the result of increased reproductive activity of worms triggered by seasonal changes. Esch and Fernandez (1993) suggested that the life cycles of hosts and parasites are synchronized since they are both responding to the same external stimuli, probably brought about by co-evolution. Alternatively, deer may be experiencing nutritional stress in spring that compromises the immune response allowing more larvae to successfully develop. Shaw and Moss (1989) concluded that the increase in numbers of Trichostrongylus tenuis eggs being released by experimentally infected red grouse (Lagopus lagopus scoticus) in the spring was due to variations in worm fecundity caused by a lowering of the hosts' resistance during a time of physiological stress associated with territorial behaviour.

A number of other closely related elaphostrongyline nematodes also exhibit a spring rise in larval output, including P. odocoilei in mule deer (Samuel et al.

1985), and P. andersoni in caribou (Rangifer tarandus groenlandicum and R. t. caribou) (see Lankester and Hauta 1989). Halvorsen et al. (1985) saw larval production of Elaphostrongylus rangiferi increase in male reindeer (Rangifer tarandus tarandus) in the fall following the rut and in females following parturition in the spring. These changes in larval output of E. rangiferi were thought to be due to reduced host resistance.

The greatest numbers of larvae were released by deer with a higher proportion of female worms in the venous blood sinuses. The blood sinuses are ideal locations for female worms since they provide a direct route for eggs travelling to the heart and lungs. Worms in the subdural space lay their eggs on the dura where they become enmeshed in fibrous tissue (Anderson 1963). Larvae that hatch on the dura may have a difficult time reaching the venous circulation and the lungs. In the present study there was no indication that more worms moved into the blood sinuses with increasing age of infection (i.e. in increasingly older deer). Similarly, Gilbert (1973) detected no differences in the location favoured by worms in relation to age of deer. Both Gilbert (1973), working in Maine, and Thurston and Strout (1978) in New Hampshire, reported the most frequent site of infection was the blood sinus within the tentorium cerebelli. Interestingly, the most common site of infection in my study were the cavernous sinuses, which are at the end of cranial venous blood flow draining into the jugular veins.

There was no correlation between the number of female worms in the

cranium and the number of larvae in the feces. Bogaczyk (1990) similarly found no correlation using the total number of worms rather than only females. Possibly, the combined effects of deer age, age of infection, season, location of female worms, and the degree of host immune response mask any correlation with numbers of female worms.

There may be an upper limit to the number of adult worms accommodated by an individual white-tailed deer and this threshold number is unaltered by increasing deer densities. Deer in a confined population reaching a year-round density of 30 animals/km^2 had the same number of adult P. tenuis in heads as deer where summer density was only 3.7/km^2. Similarly, Gilbert (1973) and Bogaczyk et al. (1993) found no correlation between deer density and the number of worms in the heads of infected deer. A threshold number of adult worms will result in similar numbers of larvae being produced by individual deer at varying densities. On the other hand, suprapopulation larval production will be related to deer density since in a dense population more animals will be releasing larvae. The mean number of larvae passed by animals in the TCAAP population, however, was greater than that by animals in the Grand Marais population. Since the mean intensity of adult worms was the same in both populations the higher larval production probably was not a direct response to deer density, but due possibly to more fecund worms in the TCAAP animals. The higher mean intensity could result from a more fecund strain of worm and/or a weaker immune response by the deer.

Over-all larval production by a deer herd could be increased if the proportion of sterile, unisexual infections in deer was reduced, thereby increasing the proportion of patent infections in the deer population. One way this might occur is as a result of increased prevalence and numbers of infective larvae in gastropods. This would increase the chances of a deer ingesting larvae of both sexes before resistance to further infection developed. Climatic conditions favouring survival of first-stage larvae, and increased abundance and movement of gastropods, could have this result.

Schmitz and Nudds (1994), in an attempt to model a P. tenuis system, pointed out that no empirical data exists on the rate of transmission of this parasite from one definitive host to another. Although, Peterson and Lankester (1991) suggested that prevalence of P. tenuis infection in fawns generally reflects the suitability of conditions for transmission among deer, their prevalence estimates were based on fecal examinations and did not detect pre-patent animals or those infected with only one sex of worm. Transmission rates of P. tenuis are best estimated by the prevalence of adult worms found in the fawn cohort. The fawns must be sampled late enough in winter to allow sufficient time for maturing worms to reach the cranium. Infection rates would be more difficult to measure in southern parts of deer range where transmission to young animals probably occurs over a longer, less well defined, time period.

In this study, 81% of fawns examined in late winter (Feb. 1 - Mar. 31) acquired infections over the summer of 1991 compared to 80% in the summer of

1992. Other studies reported that the prevalence of P. tenuis can differ significantly from year to year (Gilbert 1973, Brown 1983, Peterson and Lankester 1991, Bogaczyk et al. 1993). These variations in prevalence probably reflect differing conditions for transmission between years. Years of low rainfall presumably result in decreased survivability of first-stage larvae due to desiccation (Shostak and Samuel 1984), and decreased abundance and movement of gastropods (Lankester and Anderson 1968).

Findings reported here have important implications for modelling P. tenuis transmission within deer herds and in understanding factors that determine the risk of infection to susceptible cervids. Infrapopulation larval production may be largely independent of deer density. A threshold mean number of adult worms (3.2 ± 2.2) determines the maximum number of larvae produced per deer. Larval production is highest in young animals and in spring of the year. However, suprapopulation larval production does increase with higher deer density. As well, the proportion of young naive deer in a population and the ability of deer to produce an effective immune response to the parasite also can be expected to alter suprapopulation larval production by a deer herd. Climatic factors that increase the mean number of infective larvae per gastropod, and thereby, reduce the proportion of unisexual infections and increase the threshold intensity in deer, will also increase larval production. Further research should be directed toward understanding the ecological factors affecting the survival of first-stage larvae and the intensity of infection in gastropods as it affects transmission rates to cervid hosts.

LITERATURE CITED

Anderson, R.C. 1963. The incidence, development, and experimental transmission of Pneumostrongylus tenuis Dougherty (Metastrongyloidea: Protostrongylidae) of the meninges of the white-tailed deer (Odocoileus virginianus borealis) in Ontario. Canadian Journal of Zoology 41: 775-802.

Anderson, R.C. 1965. The development of Pneumostrongylus tenuis in the central nervous system of white-tailed deer. Pathologia veterinaria 2: 360-379.

Anderson, R.C. 1992. Nematode parasites of vertebrates: their development and transmission. Wallingford, UK. C.A.B. International. 578 pp.

Anderson, R.C., and A.K. Prestwood. 1981. Lungworms. *In*: Diseases and parasites of white-tailed deer, Davidson, W.R., F.A. Hayes, V.F. Nettles, and F.E. Kellogg (eds.). Miscellaneous Publications Number 7, Tall Timbers Research Station, Tallahassee, Florida, pp. 266-317.

Anderson, R.C., and U.R. Strelive. 1967. The penetration of Pneumostrongylus tenuis into the tissues of white-tailed deer. Canadian Journal of Zoology 45: 285-289.

Anderson, R.M., and R.M. May. 1982. Population biology of infectious diseases. Sprigner, Berlin Heidelberg, New York.

Beaudoin, R.L., W.M. Samuel, and C.P.A. Strome. 1970. A comparative study of the parasites in two populations of white-tailed deer. Journal of Wildlife Diseases 6: 56-63.

Behrend, D.F. 1970. The nematode, Pneumostrongylus tenuis, in white-tailed

deer in the Adirondacks. New York Fish and Game Journal 17: 45-49.

Behrend, D.F., and J.F. Witter. 1968. Pneumostrongylus tenuis in white-tailed deer in Maine. Journal of Wildlife Management 32: 963-966.

Bogaczyk, B.A. 1990. A survey of metastrongyloid parasites in Maine cervids. Masters Thesis. University of Maine, Maine, 59 pp.

Bogaczyk, B.A., W.B. Krohn, and H.C. Gibbs. 1993. Factors affecting Parelaphostrongylus tenuis in white-tailed deer (Odocoileus virginianus) from Maine. Journal of Wildlife Diseases 29: 266-272.

Brown, J.E. 1983. Parelaphostrongylus tenuis (Pryadko and Boev) in the moose and white-tailed deer of Nova Scotia. Masters Thesis. Acadia University, Wolfville, Nova Scotia, 136pp.

Bull, P.C. 1964. Ecology of helminth parasites of the wild rabbit Oryctolagus cuniculus in New Zealand. Bulletin 158, New Zealand Department of Scientific and Industrial Research, 147 pp.

Carreno, R.A., and M.W. Lankester. 1993. Additional information on the morphology of the Elaphostrongylinae (Nematoda: Protostrongylidae) of North American Cervidae. Canadian Journal of Zoology 71: 592-600.

Comer, J.A., W.R. Davidson, A.K. Prestwood, and V.F. Nettles. 1991. An update on the distribution of Parelaphostrongylus tenuis in the southeastern United States. Journal of Wildlife Diseases 27: 348-354.

Dew, T.L. 1988. Prevalence of Parelaphostrongylus tenuis in a sample of hunter-harvested white-tailed deer from a tri-county area in northeastern Wisconsin. Journal of Wildlife Diseases 24: 720-721.

Dougherty,E.C. 1945. The nematode lungworms of North American deer of the genus Odocoileus. Parasitology 36: 199-208.

Dudak, D., G.W. Cornwell, R.B. Holliman, and B.S. McGinnes. 1965. The incidence and degree of infection of Pneumostrongylus tenuis in the white-tailed deer of western Virginia. Transactions of the Annual Conference of the Southeastern Association of the Game and Fish Commissioners, Tulsa, OK 19: 128-141.

Esch, G.W., and J.C. Fernandez. 1993. A functional biology of parasitism: ecological and evolutionary implications. London, UK. Chapman and Hall. 337 pp.

Garner, D.L., and W.F. Porter. 1991. Prevalence of Parelaphostrongylus tenuis in white-tailed deer in northern New York. Journal of Wildlife Diseases 27: 594-598.

Gilbert, F.F. 1973. Parelaphostrongylus tenuis (Dougherty) in Maine: I - The parasite in white-tailed deer (Odocoileus virginianus, Zimmermann). Journal of Wildlife Diseases 9: 136-143.

Halvorsen, O., A. Skorping, and K. Hansen. 1985. Seasonal cycles in the output of first-stage larvae of the nematode Elaphostrongylus rangiferi from reindeer, Rangifer tarandus tarandus. Polar Biology 5: 49-54.

Jarvinen, J.A., and W.A. Hedberg. 1993. Parelaphostrongylus tenuis (Nematoda) in white-tailed deer (Odocoileus virginianus) in central Iowa. The Journal of Parasitology 79: 116-119.

Karns, P.D. 1967. Pneumostrongylus tenuis in deer in Minnesota and

implications for moose. Journal of Wildlife Management 31: 299-303.

Lankester, M.W. 1987. Pests, parasites and diseases of moose (Alces alces) in North America. Swedish Wildlife Research Viltrevy, Supplement 1, Part 2:461-489.

Lankester, M.W., and R.C. Anderson. 1968. Gastropods as intermediate hosts of Pneumostrongylus tenuis Dougherty of white-tailed deer. Canadian Journal of Zoology 46: 373-383.

Lankester, M.W., and L.P. Hauta. 1989. Parelaphostrongylus andersoni (Nematoda:Elaphostrongylinae) in caribou (Rangifer tarandus) of northern and central Canada. Canadian Journal of Zoology 67: 1966-1975.

Lenarz, M.S. 1991. Simulation of the effects of emergency winter feeding of white-tailed deer. Wildlife Society Bulletin 19: 171-176.

Peterson, B.J., and M.W. Lankester. 1991. Aspects of the epizootiology of Parelaphostrongylus tenuis in a white-tailed deer population. Alces 27: 183-192.

Prestwood, A.K. 1970. Neurologic disease in a white-tailed deer massively infected with meningeal worm (Pneumostrongylus tenuis). Journal of Wildlife Diseases 6: 84-86.

Prestwood, A.K., and V.F. Nettles. 1977. Repeated low-level infection of white-tailed deer with Parelaphostrongylus andersoni. The Journal of Parasitology 58: 897-902.

Prestwood, A.K., and J.F. Smith. 1969. Distribution of meningeal worm (Pneumostrongylus tenuis) in deer in the southeastern United States.

Journal of Parasitology 55: 720-725.

Pybus, M.J., and W.M. Samuel. 1981. Nematode muscleworm from white-tailed deer of southeastern British Columbia. The Journal of Wildlife Management 45: 537-542.

Rezac, P., P. Kindlmann, I. Dostalkova, and E. Holasova. 1993. Dynamics of gastropod infection by first-stage larvae of protostrongylid nematodes - a model. Parasitology 107: 537-544.

Samuel, W.M., T.R. Platt, and S.M. Knispel-Krause. 1985. Gastropod intermediate hosts and transmission of Parelaphostrongylus odocoilei, a muscle-inhabiting nematode of mule deer, Odocoileus h. hemionus, in Jasper National Park. Canadian Journal of Zoology 63: 928-932.

Samuel, W.M., M.J. Pybus, D.A. Welch, and C.J. Wilke. 1992. Elk as a potential host for meningeal worm: implications for translocation. Journal of Wildlife Management 56: 629-639.

SAS Institute Inc. 1985. SAS user's guide: Statistics, Version 5 ed. Cary, North Carolina, 956 pp.

Saunders, B.P. 1973. Meningeal worm in white-tailed deer in northwestern Ontario and moose population densities. Journal of Wildlife Management 33:888-894.

Schmitz, O.J., and Nudds T.D. 1994. Parasite-mediated competition in deer and moose: how strong is the effect of meningeal worm on moose? Ecological Applications 4: 91-103.

Severinghaus, C.W. 1949. Tooth development and war as criteria of age in

white-tailed deer. The Journal of Wildlife Management 13: 195-215.

Shaw, J.L., and R. Moss. 1989. The role of parasite fecundity and longevity in the success of Trichostrongylus tenuis in low density red grouse populations. Parasitology 99: 253-258.

Shostak, A.W., and W.M. Samuel. 1984. Moisture and temperature effects on survival and infectivity of first-stage larvae of Parelaphostrongylus odocoilei and P. tenuis (Nematoda: Metastrongyloidea). Journal of Parasitology 70: 261-269.

Thurston, D.R., and R.G. Strout. 1978. Prevalence of meningeal worm (Parelaphostrongylus tenuis) in white-tailed deer from New Hampshire. Journal of Wildlife Diseases 14: 89-96.

Watson, T.G. 1984. Tissue worm in red deer. Symptoms and control. AgLink FPP 249, Media Services, Min. Agr. and Food, Wellington, New Zealand.

Whitlaw, H.A., and M.W. Lankester. 1994. The co-occurrence of moose, white-tailed deer and Parelaphostrongylus tenuis in Ontario. Canadian Journal of Zoology (in press).

Zar, J.H. 1984. Biostatistical analysis, second edition. Prentice Hall, New Jersey. 718 pp.